## **Revision of the Selenodont Artiodactyls from Thomas Farm**

# THOMAS H. PATTON

THE unusual and fascinating nature of the Miocene artiodactyl fauna from the Thomas Farm quarry in north central Florida was first brought to light through a series of articles by T. E. White (1940, 1941, 1942, 1947). Although Simpson (1932) had earlier described *Oxydactylus floridanus* (=*Nothokemas floridanus*) and an indeterminate cervid from the Thomas Farm, it was only after the extensive Harvard University excavations from 1939 to 1947 that the extent of the fauna was realized.

Several Miocene and Pliocene artiodactyls occur both in Florida on the Texas Gulf Coastal Plain. Comparison of material from the two regions led to a reëvaluation of several artiodactyls from Texas and a suprageneric reallocation of some of the Thomas Farm species (Patton, 1967 and Ms). The author considers the Thomas Farm Fauna to be of Early Hemingfordian (early Middle Miocene) age.

The Miocene vertebrate faunas from the Gulf Coastal Plain of Texas and Florida are becoming sufficiently well known that a revision of at least a portion of the artiodactyl fauna would be timely and helpful to those workers not familiar with this fossil province. Earlier listings of the Thomas Farm artiodactyls are provided in Romer (1947), Ray (1957), Olsen (1962), and Patton (1964). Apparently C. Ray and B. Patterson, in an unpublished list of these forms, visualized some of the changes made below.

I should like to thank Bryan Patterson of the Museum of Comparative Zoology, Stanley Olsen of the Florida State Geological Survey, and Beryl Taylor of the Frick laboratory, American Museum of Natural History, for the generous loan of most of the fossil material discussed herein.

> Order ARTIODACTYLA Owen, 1848 Suborder TYLOPODA Illiger, 1811 Family Camelidae Gray, 1821 Subfamily Camelinae Gray, 1821

Nothokemadinae White, 1947

Genus Nothokemas White, 1947 Nothokemas floridanus (Simpson), 1932

Oxydactylus floridanus Simpson, 1932, p. 35, figs. 20-21. Paratylopus grandis White, 1940, p. 33, pl. 5, figs. A, B. Nothokemas grandis (White); White, 1947, p. 508, figs. 5-6, in part.

*Type.* FGS V-5247, part of a right maxilla with  $P^2$ -M<sup>3</sup>. Paratype, FGS V-5238, a right ramus with  $P_3$ -M<sub>3</sub>.

The genus Nothokemas was originally described by White (1947) on the basis of characters exhibited in a crushed skull, a right maxilla with  $P^2$ -M<sup>3</sup>, and several mandibles with partially preserved dentitions, all recovered from the Thomas Farm quarry, but not definitely associated. The type species of Nothokemas was designated by White (1947) as Nothokemas grandis, first described by him (1940) as Paratylopus grandis, also from the Thomas Farm.

On the basis of comparisons of specimens from the Thomas Farm and from the Garvin Gully Fauna of Texas, it is the writer's opinion that *Nothokemas grandis* White (1947) and *Oxydactylus floridanus* Simpson (1932) are synonyms. A comparison of the lower jaws of the two genera follows (all after Patton, Ms):

In the unreduced condition of the premolars and the configuration of both molars and premolars, the lower jaw of *Nothokemas* is remarkably similar to *Oxydactylus*. As in *Oxydactylus*, the body of the mandible is deep and thin, but the diastema anterior to  $P_2$  is considerably longer. The mandible in this region is much more attenuated than in *Oxydactylus*. Both genera are brachyodont and both display a relative elongation of the molars. In a specimen (MCZ 4323) referred by White (1947) to *N. grandis*, just anterior to the mental foramen there is what appears to be an alveolus for a large canine-like tooth. In a smaller and slightly dissimilar specimen (UTBEG 40067-10), assigned to *Nothokemas minimus* n. sp., a large caniniform tooth is present. Because of its position well anterior to the anterior mental foramen and the posterior border of the symphysis, I believe this tooth to be the true canine. Loss of  $P_1$ , therefore, should be included in the generic diagnosis of *Nothokemas*.

The lower molars of Nothokemas differ from Oxydactylus in the presence of an intercolumnar tubercle between the protoconid and hypoconid. The posterior edge of the entoconid of  $M_3$  overlaps the hypoconulid, giving the appearance of the beginning of an "outer lobe" on the talonid (White, 1947, p. 511).

The anterolingual fold of  $P_3$  and  $P_4$  is distinctly more pronounced in *Nothokemas* than in *Oxydactylus*. The posterolingual cusp (entoconid?) of  $P_2$  and  $P_3$  is rather strongly expressed in *Nothokemas*; In *Oxydactylus* it is distinct on three of the four specimens with  $P_3$  intact, but it has virtually disappeared from  $P_2$ , the posterolabial cusp (hypoconid?) being the only posterior cusp remaining.

Because the genus Oxydactylus is in need of revision and presently lacks taxonomic unity, this and all subsequent comparisons in this paper will be made with the following species only: O. longipes Peterson (type species), O. brachyodontus Peterson, O. campestris Cook, and O. benedentatus (Hay).

The molars of the upper jaw of *Nothokemas* differ considerably from those of *Oxydactylus*. Strongly developed stylar cusps are present on the paraselene and metaselene of *Nothokemas*, and a prominent rib extends up each selene from the base of the crown to the tip of both paracone and metacone. These features are not as well expressed in *Oxydactylus*. In addition, intercolumnar tubercles, or accessory tubercles, between the protoselene and hyposelene, completely absent in *Oxydactylus*, are a consistent character of the molars of *Nothokemas*. Prominent cingula are present among the anterior margin of the anterior crescents of  $M^1-M^3$ . On  $M^1$  of the type(FSGS V-5247) of *Nothokemas floridanus*, this cingulum extends posteriorly around the anterior crescent, and although part of the tooth is broken off in this region, it probably connected with the intercolumnar tubercle.

The upper premolars of *Nothokemas* are unusually large and robust.  $P^2$  and  $P^3$  are both proportionally longer and wider than those teeth in *Oxydactylus*.  $P^2$  of *Nothokemas* also differs from that of *Oxydactylus* in its relatively greater size and in the greater development of the anterolabial flexus and the internal cingulum.

In summary, the long diastema anterior to  $P_2$ , loss of  $P_1$ , the posterior extension of the entoconid on  $M_3$ , the presence of intercolumnar tubercles on the upper and lower molars, the greater development of the posterolingual cusp on  $P_2$  and  $P_3$ , and the more pronounced anterolabial flexus and internal cingulum on  $P^2$ , all serve to separate Nothokemas from Oxydactylus. The systematic affinities of Nothokemas are discussed below in the section on Floridatragulus.

A partial left maxilla with  $dP^{2-4}$ -M<sup>1</sup> (MCZ 4328), referred by White (1947) to *Nothokemas grandis*, is placed here in *Prosynthetoceras texanus*. I have not examined two additional specimens. These are a partial skull (MCZ 4329) and a partial right maxilla (MCZ 4322).

# Subfamily Floridatragulinae new subfamily Genus Floridatragulus White, 1940 Floridatragulus dolichanthereus White, 1940

Floridatragulus dolichanthereus White, 1940, p. 35. Hypermekops olseni White, 1942, pp. 11-13, pl. 9, figs. 1-3.

*Type.* MCZ 3635, a partial mandible with right and left  $M_1$ - $M_3$ . White described the genus *Floridatragulus* from material recovered from the Thomas Farm deposits and designated *Floridatragulus dolichanthereus* as the type species. His generic diagnosis was given as follows:

A large brachyodont hypertragulid with a very long mandibular symphysis, diastema between  $P_2$  and  $P_3$  equal to two thirds of that between  $P_1$  and  $P_2$ , basal pillars of molars low and elongate antero-posteriorly, 'heel' of  $M_3$  divided so that it forms two grinding crescents.

In 1942, White described *Hypermekops* on the basis of a skull containing  $I^{1-2}$ ,  $P^2$  and  $P^4$ , and  $M^{1-3}$  of the right side, and  $I^1$  and  $P^4$  to  $M^3$  on the left side. *Hypermekops olseni* was designated the type species. White's generic diagnosis of *Hypermekops* was given as follows:

A large brachyodont hypertragulid with three incisors in the premaxillary, fourth premolar and molars similar in form to those of *Leptomeryx*,  $P^3$  three rooted and probably with a median spur,  $P^2$  double rooted, elongate anteroposteriorly and without median spur,  $I^1$  to  $P^1$  caniniform and slightly recurved,  $I^1$  largest.

Although White (1942, P. 13) was aware that *Hypermekops* and *Floridatragulus* were closely related (he inferred on the basis of snout length that *Floridatragulus* was derived from *Hypermekops*), the lack of a comparable material available at that time precluded closer comparison of the two genera. On the basis of a skull and jaw of *Floridatragulus* collected from the Thomas Farm in 1964 by Stanley Olsen (now in the Frick Collection of the AMNH), it now is possible to state that the skull assigned by White (1942) to *Floridatragulus* clearly belongs to the same species. *Hypermekops olseni* is thus a synonym of *Floridatragulus dolichanthereus*. A similar conclusion has been reached by Clayton Ray and by Bryan Patterson in unpublished studies of these forms (McKenna, 1966).

The skull and jaw collected by Olsen were not actually articulated but were recovered from the same part of the Thomas Farm quarry (S. J. Olsen, personal communication). The size, preservation, degree of tooth wear, extreme length of snout, and correspondence of occluding surfaces of these two specimens indicate that they belong to the same individual. No other Thomas Farm artiodactyl shows such remarkable morphological similarity to these specimens. P3 in MCZ 3711 is represented only by alveoli. P2 in both specimens is slender, distinctly tricuspate, and has a weak internal cingulum. More compelling evidence for the identity of these two taxa is seen in the long, attenuated snout of both. In the better preserved specimen (MCZ 3711) the elongated muzzle possesses four caniniform teeth or alveoli. White (1942, p. 11-12) interpreted these as representing  $I^1$ - $I^3$ , C/, and P<sup>1</sup>. The largest caniniform tooth in this series, according to White's interpretation, would be I<sup>2</sup>. In the Frick specimen alveoli for the only two caniniform teeth occur between P<sup>3</sup> and the largest caniniform. What appears to be the maxillo-premaxillary suture in this specimen is located just anterior to the large caniniform tooth. If the maxillopremaxillary suture can be used to separate  $I^3$  and C/, the anteriormost tooth in this series would be I<sup>3</sup>, the second (just posterior to the maxillo-premaxillary suture) would be the upper canine, and the subsequent three (on MCZ 3711) alveoli probably would represent a deciduous canine, P1, and deciduous P1. The presence of only two alveoli posterior to C/ in the Frick specimen indicates that the retention of the more posterior deciduous teeth is somewhat variable. In any event, it is clear that the two skulls are too similar to regard as representing separate taxa.

#### Floridatragulus barbouri White, 1947

Floridatragulus barbouri White, 1947, p. 505, fig. 4.

Two species of *Floridatragulus* are recognized in the Thomas Farm Fauna, *F. dolichanthereus* White and *F. barbouri* White. *Floridatragulus dolichanthereus* differs from *F. barbouri* in its larger size and in having a longer diastema between  $P_2$  and  $P_3$ . Remains of *Floridatragulus* are not abundant in the Thomas Farm deposits, and the sample available is small, but the differences appear to be constant. Perhaps separation of the two species is justified best by their stratigraphic occurrence.

It is uncertain whether F. dolichanthereus and F. barbouri lived contemporaneously, or whether they represent an actual ancestordescendent lineage. The nature of the Thomas Farm deposit and the history of its excavation (White, 1942; Bader, 1956) suggest that those forms as they are known so far were separated temporally. The largest species, F. dolichanthereus, was recovered from the uppermost layers of the deposit and has not been found in any of the deeper sediments (White, 1942, p. 30). The smaller less advanced F. barbouri was recovered from a deeper portion of the quarry. Hence, there is reason to accept the second alternative; that F. barbouri is a representative of an earlier group which evolved (there is no evidence to suggest replacement) into F. dolichanthereus.

Other evidence, based on associated fossil horses, also suggests that the Thomas Farm fauna is heterochronic (Bader, 1956; Patton, 1964).

Other floridatragulines are present in Miocene deposits in the Texas Coastal Plain (Patton, Ms). An as yet unstudied specimen from the Garvin Gully Fauna appears to be similar to *Floridatragulus barbouri*, and *F. dolichanthereus* corresponds closely to *F. texanus* from the Burkeville Fauna, differing from that species only in having smaller premolars and a more invaginated talonid on  $M_3$ . A still larger form, *F. hesperus*, occurs in the Texas Cold Spring Fauna; it has no known counterpart in Florida.

Discussion. Systematic placement of the Floridatragulinae is uncertain. To date only relatively fragmentary and unassociated material from Miocene deposits in Texas and Florida has been studied and, expectedly, has revealed little in the way of phyletic clues. Fortunately, skull and jaw material from the Thomas Farm is now available, and it is hoped that study of this material will help in understanding the puzzling systematics of this group. A few preliminary remarks are in order, however.

Floridatragulus bears considerable resemblance to members of two families of artiodactyls, the Hypertragulidae and the Camelidae. Floridatragulus resembles members of the Hypertragulidae in the presence of the intercolumnar pillars, a double enamel loop on the heel of  $M_3$ , rather prominent cingula, and in the occurrence of a diastema between  $P_2$  and  $P_3$ . In the hypertragulids the detached  $P_2$  tends to be unicuspid; in Floridatragulus this tooth is bicuspid, though weakly so. The anterior lower premolars of Floridatragulus are laterally compressed as in camels, and  $P_4$ , although more foreshortened than in most camels, retains the general features of that group. In the skull and jaws of Floridatragulus from the Thomas Farm, now in the Frick Laboratory, the extremely elongated muzzle has four caniniform teeth (or alveoli) on each side, probably representing modifications of the incisors, C/, and P<sup>1</sup>. This is a characteristic feature of the Tylopoda, in which the upper incisors and anterior premolars may undergo reduction, but in which there is never a complete loss of the upper incisors. In contrast, the hypertragulids are marked by either extreme reduction or complete suppression of the upper incisors, although they may be retained in some of the very primitive types.

Because of its similarity to the camels, but also because of its distinctness within that group, I have referred Floridatragulus to the Camelidae but as a separate subfamily. Certainly those characters which distinguish it from the Camelinae are equivalent in taxonomic weight to those of other camel subfamilies, even, for example, the Stenomylinae. Perhaps for parallel reasons, White (1947) tentatively placed the genus *Nothokemas* (as the type of a new family) in the Hypertragulonidea. Of these two problematical genera, Nothokemas more closely approximates the features of the Camelidae. In the unreduced condition of the premolars and the configuration of both molars and premolars, the lower jaw of Nothokemas is remarkably similar to Oxydactylus. As in Oxydactylus, the body of the mandible is deep and thin, but the diastema anterior to  $P_2$  is considerably longer. The mandible in this region is much more attenuated than in Oxydactylus. Both genera are brachvodont and both display a relative elongation of the molars

In addition, if the skull (MCZ 4329) assigned to Nothokemas by White (1947) does in fact belong to that genus, it can be seen to possess a closed orbit, a more advanced feature not shared by *Floridatragulus*. Although certain primitive characters possessed by both Nothokemas and *Floridatragulus* are shared by members of the Hypertraguloidea, e.g., intercolumnar tubercles, they are not restricted to that group but may be regarded as archaic traits retained by several disparate artiodactyl groups, including the Camelidae. The increase in similarity between the camels and hypertragulids as we look further back in geologic is well documented (Scott, 1940; Matthew, 1905; Colbert, 1941; Simpson, 1945). The two divergent groups are supposedly recognizable as early as the Late Eocene, but in the Middle Miocene of the Gulf Coastal Plain we have two genera which share few features in common with any of the contemporary representatives of those basal stocks. Nothokemas conceivably could be derived from some early Oxydactylus, but that genus seems too advanced to have provided an ancestor for Floridatragulus. Whether or not the morphological similarity between either one or both of the Gulf Coast genera and some members of the Camelidae is the result of recent common descent, parallelism, or convergence is too fine a distinction to make with the information available. However, the possibility remains that both genera are descendants of an early and distinct branch off the tylopod lineage which became isolated in the Gulf Coastal Plain and occupied an adaptive zone in this region similar to that occupied by some camels in the Great Plains. With the invasion of the Gulf Coast by several diversified camel genera from the Great Plains during the Early Pliocene or slightly earlier, the autochthonous Gulf Coast genera became extinct.

> Suborder RUMINANTIA Scopoli, 1777 Infraorder TRAGULINA Flower, 1883 Family **Protoceratidae** Marsh, 1891 Genus *Prosynthetoceras* Frick, 1937 *Prosynthetoceras texanus* (Hay), 1924

Dromomeryx texanus Hay; Hay, 1924, p. 15-16, pl. 11, figs. 8-12.
Dromomeryx angustidens Hay; Hay, 1924, p. 16, pl. 11, figs. 6-7.
Merycodus grandis Hay; Hay, 1924, p. 17-18, pl. 111, figs. 9-11.
Protolabis francisi Hay; Hay, 1924, p. 14, pl. 111, figs. 5, 6. (in part).
?Cranioceras texanus (Hay); Frick, 1937, p. 82, 97.
?Synthetoceras rileyi Frick; Frick, 1937, p. 603, 605, fig. 66.
Blastomeryx texanus (Hay); Wood and Wood, 1937, p. 137, pl. 1, figs. 5, 6.
?Syndyoceras texanus (Hay); Hesse, 1942, p. 163 (?Syndeoceras texanus, p. 167, lapsus).
Syndyoceras (Prosynthetoceras) douglasi White, 1947, p. 504, fig. 3a.

cf. Miolabis sp. indet., Simpson, 1932, p. 37.

cf. Miolabis tenuis, Ray, 1957, p. 18.

Nothokemas grandis White, 1947, p. 508. (in part).

Type. TAMU 2387, a right  $M^3$  from the Garvin Gully Fauna of Texas.

Two genera of synthetocerines, *Syndyoceras* and *Synthetoceras* (*Prosynthetoceras*), have been recognized from fossil material recovered from the Thomas Farm. In 1941, white described *Syndyoceras australis* on the basis of a right lower jaw with  $P_1$  and  $P_4$ - $M_3$  (MCZ 3654, type), and a left maxilla with  $P^3$ - $M^2$  (MCZ 3642, para-

type). He also referred to this species three right mandibles and a core of a postorbital horn. In 1947, White described *Synthetoceras* (*Prosynthetoceras*) douglasi from a badly crushed palate with  $P^3$ - $M^3$  of both sides.

A comparison of the Thomas Farm specimens with material from the Garvin Gully and Burkeville faunas of Texas shows that the specimens assigned to S. australis White and P. douglasi White are inseparable from *P. texanus* (Hay) and should be included in the synonymy of that species. In cusp morphology as well as in dimensions of the teeth and jaws, there appear to be no significant differences between and among the specimens from both areas. Inasmuch as I have not seen the horn core White (1942) referred to Syndyoceras australis (it was not illustrated by White), no comparisons could be made with the Texas material. However, the horns, especially the rostral horn, of Prosynthetoceras texanus are considerably advanced over those of Syndyoceras cooki from the Great Plains. The evolution of the rostral horn of the synthetocerines has involved primarily the lengthening of the main shaft, resulting in an increase in the distance from the base of the rostral horn to the point of bifurcation. In Syndyoceras the point of bifurcation is very close to the base of the horn; in fact the horns flare away from each other at the point of union just above the nasal passage. The rostral horn of *Prosynthetoceras*, on the other hand, has lengthened to the degree where there is a definite shaft between the maxillary union and the point of bifurcation.

In 1932, Simpson referred several teeth (FSGS V-4970) from Midway, Florida, to the genus *Miolabis* but considered the species indeterminate. He regarded these specimens as bearing considerable resemblance to *Miolabis tenuis*, but declined to designate them as such. Ray (1957) lists this reference as "cf.*Miolabis tenuis*." A comparison of the original specimens from Midway with material from Thomas Farm and Garvin Gully and Burkeville faunas reveals no significant difference in size or morphology between the teeth referred to *Miolabis* and those confidently assigned to *Prosynthetoceras texanus*. Although isolated molars of *Prosynthetoceras* and *Floridatragulus* are very similar in morphology, those of *Floridatragulus* are considerably larger than those of *Prosynthetoceras* in beds of the same age. For this reason, I have included White (1947) to *Nothokemas grandis* is assigned to *P. texanus*. A partial left maxilla with  $dP^{2-4}$ - $M^1$  (MCZ 4328) referred by White (1947) to Nothokemas grandis is assigned to *P. texanus*. This immature dentition is far too small to belong to Nothokemas but compares very closely to specimens of *P. texanus* from Texas deposits.

For reasons I have given elsewhere (Patton, in press) I believe that the elevation of *Prosynthetoceras* to generic rank more accurately reflects its relative position in the taxonomic hierarchy of the Synthetoceratinae. Thus, the synthetocerine material from the Garvin Gully and Burkeville faunas of Texas and that from the Thomas Farm of Florida are considered by the writer to belong to a single species, which on the basis of priority, is designated *Prosynthetoceras texanus*.

> Infraorder PECORA Linnaeus, 1758 Family Cervidae Gray, 1821 Genus *Blastomeryx* Cope, 1877

Blastomeryx Parablastomeryx floridanus (White), 1940, p. 34.

The larger deer specimens from the Thomas Farm, including not only White's type (MCZ 3626) but several other specimens in the collections of the University of Florida and the Florida State Geological Survey, are all characterized by a relatively short postsymphysial diastema. If Frick's (1937) criteria for separating genera in his Division Blastomerycini are applied, the Thomas Farm specimens would be assigned to the genus *Parablastomeryx*, which White (1940) did. The systematics of this group, however, is clearly in need of revision and, accordingly, it is often difficult to decide on supraspecific placement. Not only is the validity of certain morphological criteria in question, but the relative weight of Frick's supraspecific categories is sometimes indeterminable and unmanageable. Until the confusion is removed, it seems advisable to defer judgment on this assignment.

> Genus Machaeromeryx Matthew, 1926 Machaeromeryx gilchristensis White, 1941

Machaeromeryx gilchristensis White, 1941, p. 97, pl. 14, fig. 5

Generic assignment for this tiny ruminant appears to be valid. However, because of the scanty and fragmentary nature of the Thomas Farm specimens specific comparisons between it and specimens assigned to the type species from the Upper Harrison beds of Nebraska are not likely to be particularly useful. In view of the great geographic separation between the two occurrences, specific differentiation is probable.

In summary, the revised list of selenodont artiodactyls of the Thomas Farm Fauna is as follows:

Family Camelidae

Subfamily Camelinae Nothokemas floridanus (Simpson), 1932

Subfamily Floridatragulinae<sup>1</sup>

Floridatragulus dolichanthereus White, 1940 Floridatragulus barbouri White, 1947

Family Protoceratidae

Prosynthetoceras texanus (Hay), 1924

Family Cervidae

Blastomeryx gilchristensis White, 1941 Machaeromeryx gilchristensis White, 1941

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<sup>&</sup>lt;sup>1</sup>Through coincidence while this paper was passing through the press, the subfamily Floridatragulinae was described as new by another author, Vincent Joseph Maglio (A revision of the fossil selenodont artiodacytls from the Middle Miocene Thomas Farm, Gilchrist County, Florida, Breviora, Museum of Comparative Zoology, no. 255, pp. 1-27, figs. 1-4, "December 6, 1966," [postmarked January 20, 1967]).

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Florida State Museum and Department of Zoology, University of Florida, Gainesville, Florida.

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